



Research, part of a Special Feature on [Risk mapping for avian influenza: a social-ecological problem](#)
Risk Mapping of Highly Pathogenic Avian Influenza Distribution and Spread

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ABSTRACT. The rapid emergence and spread of highly pathogenic H5N1 avian influenza begs effective and accurate mapping of current knowledge and future risk of infection. Methods for such mapping, however, are rudimentary, and few good examples exist for use as templates for risk-mapping efforts. We review the transmission cycle of avian influenza viruses, and identify points on which risk-mapping can focus. We provide examples from the literature and from our work that illustrate mapping risk based on (1) avian influenza case occurrences, (2) poultry distributions and movements, and (3) migratory bird movements.

Key Words: *avian influenza; land birds; poultry; risk mapping; wild birds.*

INTRODUCTION

The 1997 emergence and rapid spread of the highly pathogenic avian influenza strain H5N1, hereafter HP-H5N1, raised concerns regarding the potential for a global influenza pandemic (Cox and Subbarao 2000, Webby and Webster 2001, Capua and Alexander 2002). The impressive virulence of this strain, both for humans (Katz et al. 2000, Parry 2006) and for some birds (Sturm-Ramirez et al. 2004, Chen et al. 2005, Olsen et al. 2006), combined with its rapid spread across Asia (Chen et al. 2005), Africa (Ducatez et al. 2006), and Europe (Alexander 2007), indeed is cause for concern. To optimize response, forecasting and tracking the global spread of HP-H5N1 becomes of key importance, particularly in light of the diversity and contrasts of opinions that have been expressed regarding its transmission (ABC 2005, Chen et al. 2005, BirdLife International 2006, Gilbert et al. 2006, Rappole and Hubalek 2006).

In spite of the importance of forecasting and anticipating the global spread of such an important pathogen, few efforts have been made to map and forecast HP-H5N1 risk across broad regions or continents. Several publications have reviewed the HP-H5N1 situation (Alexander 2000, Feare and Yasue 2006, Olsen et al. 2006, Rappole and Hubalek 2006), but only in broad and general terms. Only a

few have made more quantitative predictions or risk maps: poultry-based spread in the Netherlands (Boender et al. 2007), connections with rice cultivation in Thailand (Gilbert et al. 2007), mapping and monitoring of bird migration in various regions (Gilbert et al. 2006, Peterson et al. 2007, Winker et al. 2007), niche-based predictions of HP-H5N1 transmission risk across West Africa (Williams et al. 2008), and some more limited analyses that will not be treated in detail herein (Guo et al. 2006, Mulatti et al. 2007). Only one analysis (Kilpatrick et al. 2006) has addressed HP-H5N1 spread globally.

In this overview, we briefly review HP-H5N1 transmission routes and offer an overview of risk-mapping approaches that may be applicable to the situation. We provide examples of several such approaches, and explore how HP-H5N1 risk mapping may be improved in the future. Perhaps most importantly, given the paucity of detailed and quantitative information available, we outline how risk mapping and broad influenza monitoring can and should be linked in coming years to provide a more dynamic, responsive information base for decisions and initiatives related to HP-H5N1 and other emerging bird-borne diseases.

HP-H5N1 Transmission

The basic elements of the HP-H5N1 transmission cycle are fairly well understood (Fig. 1): in general, the virus is transmitted from bird to bird without intermediate vectors, but it can be held in bodies of water for some period of time, and mammals, including humans, are occasionally infected. Mammal-to-mammal, including human-to-human, transmission appears rare, as essentially all known human cases have some more or less direct contact with birds, usually poultry, and thus a clear connection to the bird-driven transmission cycle. Some indications of mammal-to-mammal transmission do exist (Thanawongnuwech et al. 2005), but these transmission chains are not self-sustaining.

Although the elements of the transmission cycle are not in much doubt, their relative roles are the topic of considerable debate. Some of those who opine about the topic believe fervently that the entire system is driven by movements of poultry and poultry products, and that wild birds are incidental hosts with little importance in overall HP-H5N1 transmission dynamics (BirdLife International 2006, Feare and Yasue 2006, Rappole and Hubalek 2006, Gauthier-Clerc et al. 2007) – we can term this opinion that of “wild birds as victims.” A key point revealed by inoculation studies is that at least some wild birds can be infected without significant external symptoms or death (Brown et al. 2006, Boon et al. 2007), suggesting that they can serve as carriers for avian influenza viruses once infected, potentially even on migration. On the other side of the debate, several researchers have recognized significant roles for wild birds, e.g., “wild birds as vectors,” in HP-H5N1 transmission and spread (Chen et al. 2005, Gilbert et al. 2006, Kilpatrick et al. 2006, Olsen et al. 2006, Winker et al. 2007), although poultry clearly play a role in this process as well. A recent commentary pointed out the relative costs of choosing the wrong null hypothesis in this debate, suggesting that the most appropriate presumption would be that migratory birds are involved (Flint 2007). The most balanced and the only global analysis to date (Kilpatrick et al. 2006) concluded that both domestic and wild birds have played roles in the global spread of HP-H5N1.

Still more shrouded in shadows, however, is the avian taxonomic distribution of host relationships of HP-H5N1 transmission and spread. The standard review of influenza ecology and host distribution (Webster et al. 1992) states clearly that waterbirds

are the reservoir of avian influenza viruses, and papers in the field almost invariably cite this paper and assume this point to be well established. Although influenza prevalences are clearly highest in waterbirds (Webster et al. 1992, Olsen et al. 2006, Munster et al. 2007), the occurrence of this virus in landbirds should not be neglected in surveillance efforts (Alexander 2000, Kou et al. 2005, Kwon et al. 2005, OIE 2005). Recent inoculation experiments have indicated that landbirds can be infected and can become viremic to the point of being infective to other individuals, albeit not commonly (Boon et al. 2007). Particularly of concern is the fact that major monitoring initiatives are focusing only or chiefly on waterbirds (Gaidet et al. 2007, Winker et al. 2007): appreciating a significant role for landbirds becomes difficult or impossible when they are not even being sampled.

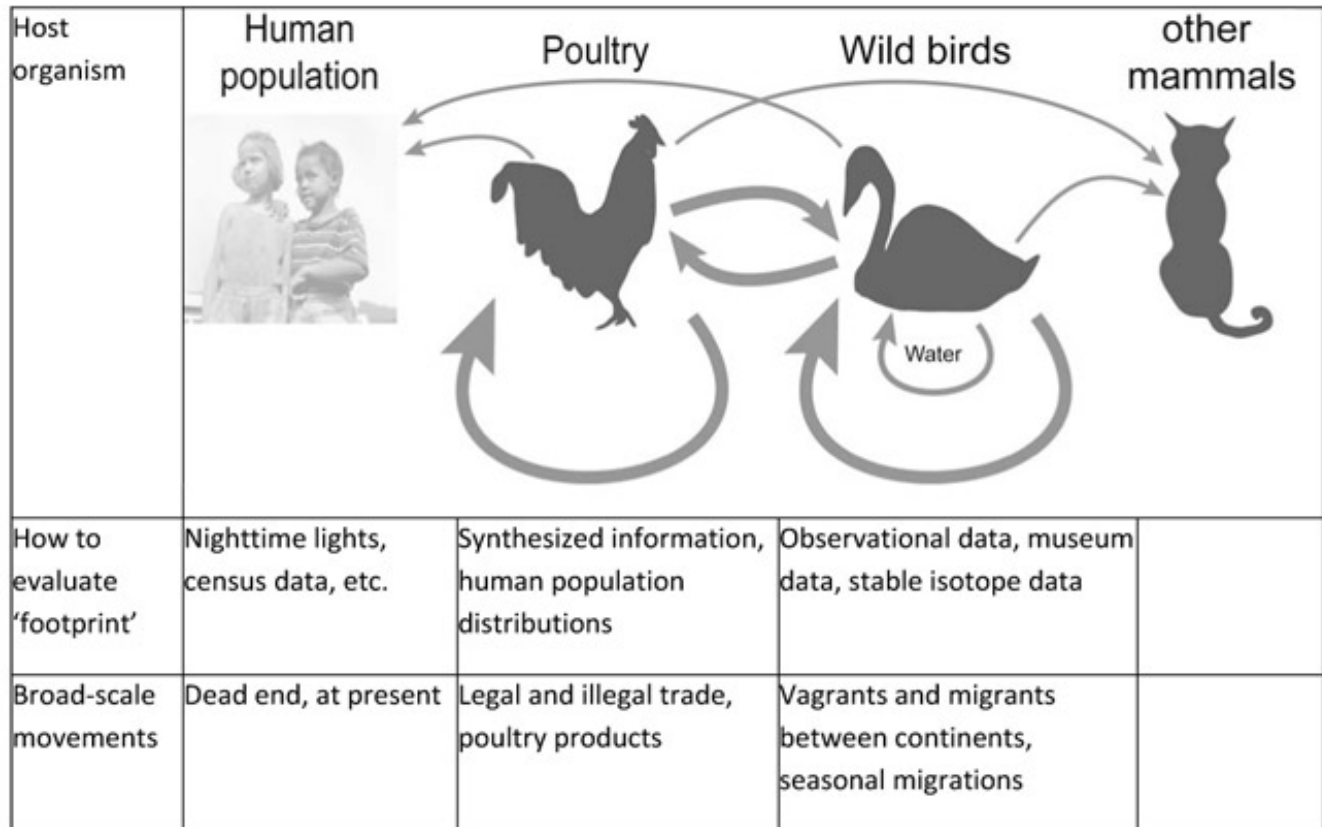
Mapping HP-H5N1 risk of transmission and spread

Three sectors of the HP-H5N1 transmission cycle may be tractable to risk mapping (Fig. 1): distributions and movements of human populations, poultry, and wild birds. In each case, broadly available data sets offer means of summarizing the distribution and movements in those elements (Fig. 1): nighttime lights and census data track human populations; specifically synthesized data or human population surrogate information can key to poultry distributions; and observational data, natural history museum data, and other ornithological data sets can inform regarding bird distributions and movements. As such, ample information resources exist on which to base risk-mapping efforts.

Three points in the transmission cycle of HP-H5N1 offer opportunities for risk mapping: (1) mapping actual cases of HP-H5N1 and extrapolating to identify areas that are similar environmentally; (2) mapping movements and commerce in poultry and poultry products; (3) mapping wild bird migration patterns, potentially educated by information from ongoing monitoring efforts. We review each of these opportunities in the paragraphs that follow, illustrating each with examples, and identifying paths toward further improvement.

An alternative approach, not explored or discussed in detail herein, is the risk analysis approach, in which hazard identification, risk assessment, management, and communication are outlined. This

Fig. 1. Diagrammatic summary of transmission routes of avian influenza viruses, showing major transmission routes (thick arrows) and minor transmission routes (slender arrows).



suite of ideas has been applied to avian influenza transmission in Ethiopia (Goutard et al. 2007) and Vietnam (Pfeiffer et al. 2007), and might be useful in refining and improving the more elemental, process-based mapping attempts outlined herein. That is to say, while we do not discount the utility of this approach, we feel that it is not sufficiently connected to HP-H5N1 transmission biology to form the basis for full risk assessments.

Finally, we note that low-pathogenic influenzas can be more numerous than the high-pathogenic viruses, and can thus provide much more abundant information regarding their ecology and distribution. HP-H5N1 is still relatively rare, and is restricted to the Old World, and detections are consequently quite rare, limiting opportunities for detailed study. As low-pathogenic strains can evolve into high-

pathogenic forms (Chen et al. 2004), their detailed study is more than warranted, although differences in transmission should be borne in mind. Research attention should thus not focus only on HP-H5N1, but should extend to avian influenza viruses in general, so as to maximize the information gained and its utility in understanding a complex situation.

Mapping HP-H5N1 cases

The simplest approach to risk mapping is that of treating the entire transmission cycle effectively as a black box, and simply focusing on the spatial position and environmental characteristics of sites where humans or poultry contract the disease (Peterson 2006). This approach has the advantage of accessing a maximum of information, i.e., any

site where the disease has been detected. However, it should be borne in mind that it integrates across all of the diverse processes that make for such an occurrence being detected, that is, biases at any point from the pathogen itself through to diagnosis and reporting can create a nonrandom distribution that appears predictive (Peterson 2006, 2008). As such, independent testing and repeated challenging of models to be predictive and general are central to this application of risk mapping.

Given the simple, bird-to-bird transmission cycle of HP-H5N1, and given the broad spectrum of birds apparently involved, i.e., both poultry and wild birds, it might be expected that no clear ecological signature would be detectable. Curiously, though, the two detailed analyses that have been developed along these lines (Gilbert et al. 2007, Williams et al. 2008) have both found significant, predictive environmental signals indicative of higher risk of HP-H5N1 transmission. Clearly, this area of risk mapping for HP-H5N1 demands more attention to determine whether it is simply tracking inherent, but subtle, biases in occurrence data, or whether the environmental signals are genuinely associated with HP-H5N1 transmission.

The first “black box” study focused on free-ranging domestic duck populations in Thailand (Gilbert et al. 2007). The tie between HP-H5N1 transmission and free-ranging domestic duck populations was already well established (Hulse-Post et al. 2005), so the novelty of this study hinges on identification of coarse-scale environmental signals of domestic duck populations that are detectable repeatably and quantitatively in remotely sensed imagery (Gilbert et al. 2007). The study resulted in clear “signatures” of domestic duck populations related to the length of the growing season for second rice plantings and harvest in Thailand, suggesting that HP-H5N1 transmission risk can be mapped successfully, at least in Southeast Asia, where duck production is so key.

The second such study (Williams et al. 2008) is much less clear mechanistically as to why risk mapping should be possible. Here, the authors focused on HP-H5N1 occurrences in Nigeria, where poultry flocks are not clearly and consistently associated with such a prominent landscape feature as rice cultivation. Using tools for ecological niche modeling (Peterson 2006), they related sites of known occurrence to a set of remotely sensed images summarizing month-to-month variation in

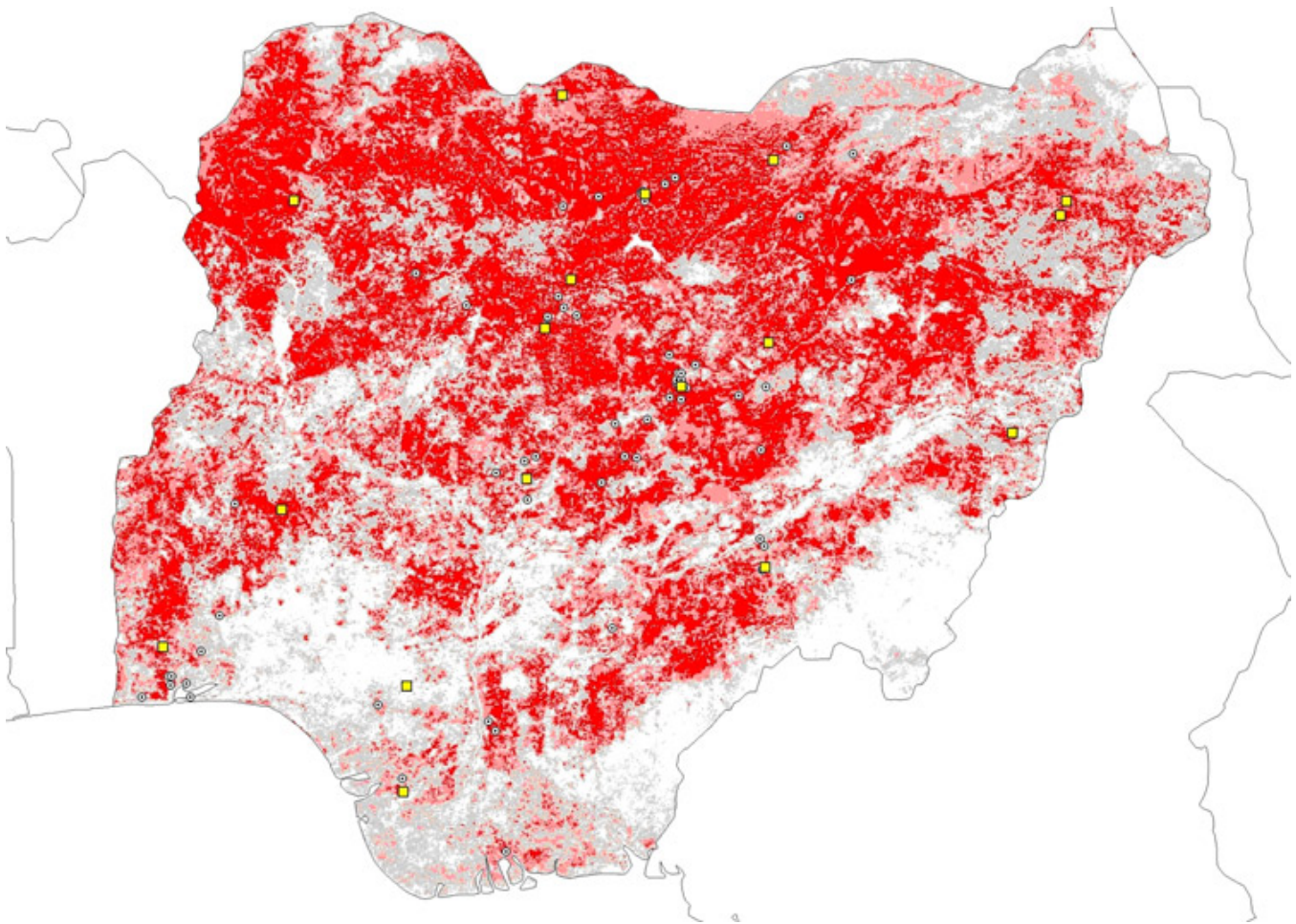
“greenness” (normalized difference vegetation index); models were challenged to predict broad sectors of the country and of West Africa from which occurrence data were withheld in the modeling process. The models, perhaps somewhat surprisingly given the lack of easily detectable environmental signals, e.g., rice paddies, were able to predict the great majority of independent occurrences in numerous tests (see Fig. 2 for an example); nonetheless, considerable additional testing is necessary before such analyses can be considered to be genuinely predictive of HP-H5N1 transmission potential.

This sort of black-box risk mapping works only if consistent environmental signals are associated with HP-H5N1 transmission, and, of course, it can be applied in a region only when some number of occurrences has already occurred. In the case of individual species’ distributions, the niche-modeling approach functions admirably thanks to species’ ecological niches (Pulliam 2000, Soberón and Peterson 2005, Soberón 2007). For HP-H5N1, however, the case is less clear, as the black box subsumes many and very diverse species and processes, except in the clearest cases, such as the rice-paddy duck production in Southeast Asia. The environmental signal, in essence the “ecological niche” of the transmission cycle, could come from some environmentally-constrained step in the cycle, or it could come from some consistent source of bias in sampling or reporting. Clearly, this area of HP-H5N1 risk mapping will require further testing and experimentation before it can be considered as a reliable source of information.

Mapping poultry movements

Moving away from simple, black-box approaches, an important element in HP-H5N1 transmission is movements of poultry and poultry products. As has been noted frequently (Kilpatrick et al. 2006), this element in the transmission cycle is difficult to quantify and map in detail owing to the combination of local, unregulated movements and trade in poultry by peasant farmers, and the broader-scale, illicit bird trade (Van Borm et al. 2005). Consequently, detailed considerations of this factor are complex, and only two previous HP-H5N1 risk-mapping efforts have included dimensions of poultry movements (Kilpatrick et al. 2006, Boender et al. 2007).

Fig. 2. Example prediction of HP-H5N1 occurrences in poultry in Nigeria (Williams et al. 2008). Dotted circles indicate 72 occurrences in January–November 2006 that were used to train the model. Model predictions are summarized as a ramp of colors, ranging from white (all replicate models agreed in predicting absence) to red (all replicate models agreed in predicting potential for presence). Yellow squares indicate independent occurrences from November 2006–January 2007 that were used to test the model predictions. Note the close correspondence between the spatial position of these occurrences and the red areas, which was statistically significantly better than random.

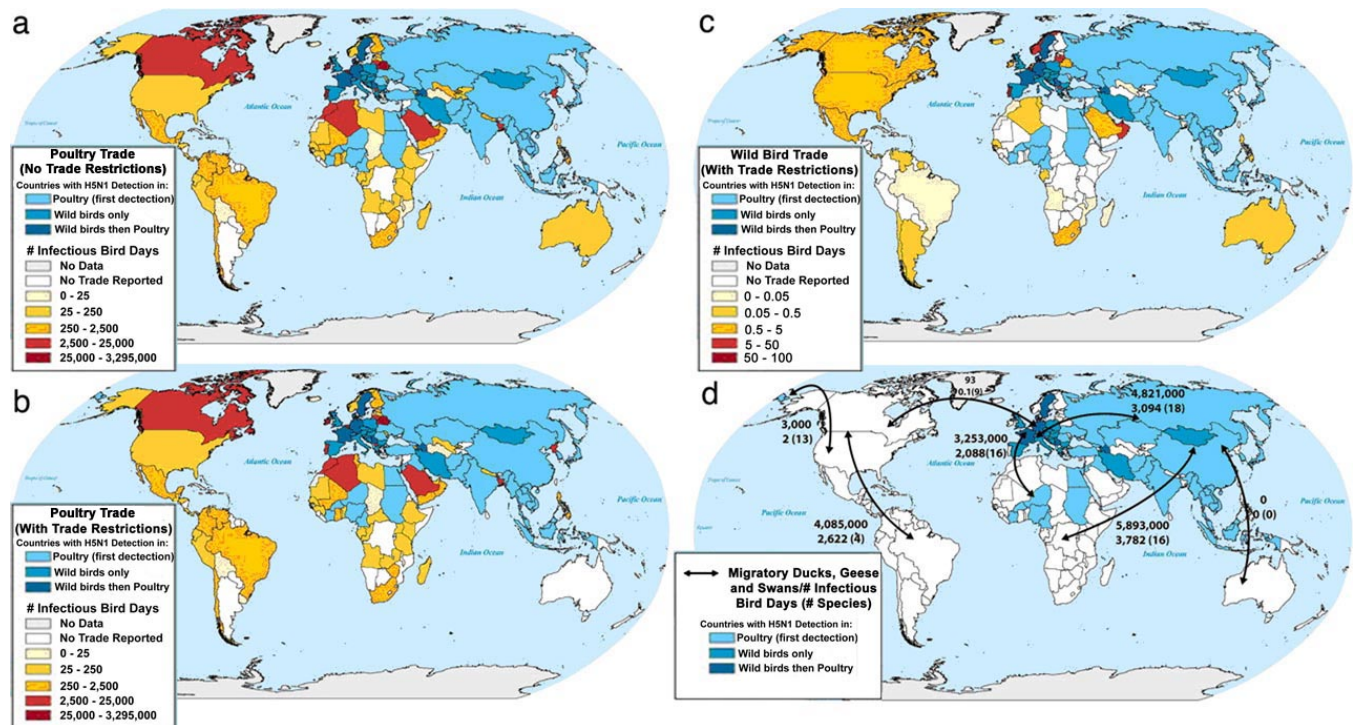


Boender et al. (2007) developed scenarios of spread of highly pathogenic avian influenza based on the spatial distribution of infected and uninfected poultry farms in the Netherlands, estimating farm-to-farm transmission probabilities based on inter-farm distances. The resulting risk maps are sensitive to parameter estimates, which become less precise when based on less-complete data. However, the principal limitation of this approach is that of obtaining detailed locations of all relevant poultry

farms in a region, particularly when study regions are broad and cross multiple states or countries.

The second poultry-based risk mapping effort is the global HP-H5N1 risk evaluation of Kilpatrick et al. (2006). Combining information on legal poultry trade with information on bird migration (see separate discussion below), this analysis produced country-level maps of the chances of HP-H5N1 introduction (Fig. 3), and offered several novel

Fig. 3. Predicted risk of HP-H5N1 introduction from countries that have had H5N1 outbreaks (in blue). (a–c) Risk was estimated as number of infectious bird days caused by trade in: live poultry with no trade restrictions (a), live poultry with no exports from countries reporting H5N1 in poultry (b), and captive wild birds with no exports from countries reporting H5N1 in poultry (c) as in b. (d) Estimated number of ducks, geese, and swans migrating between mainland continents, number of infectious bird days, and number of species (in parentheses). Reproduced from Kilpatrick et al. (2006).

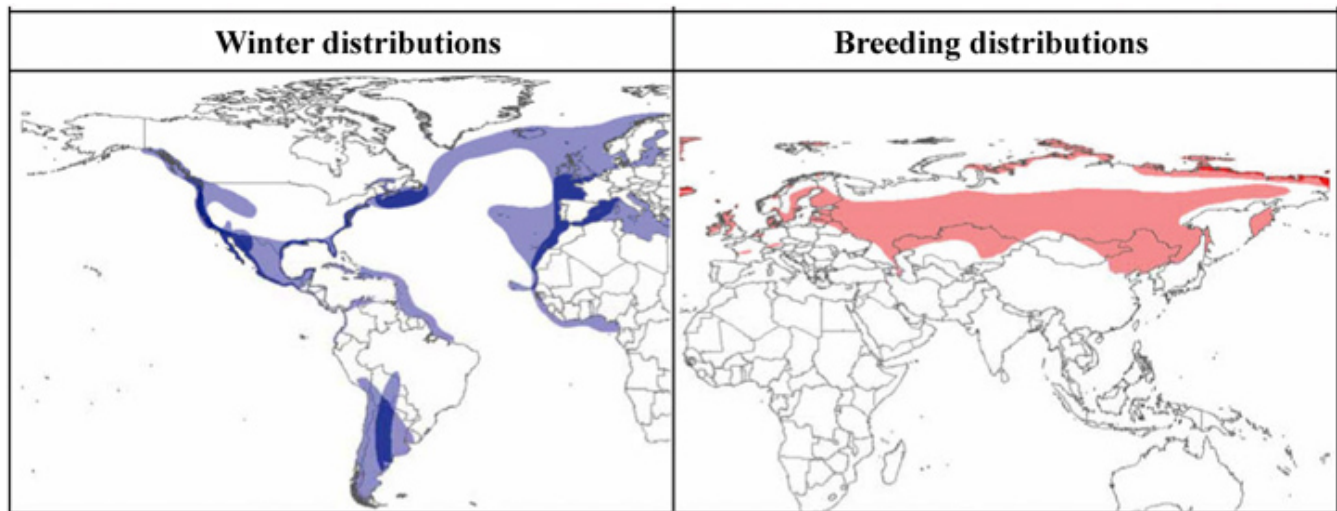


insights into introduction potential, e.g., risk of introduction into North America via South America. This study was limited in several dimensions, particularly in its focus on legal poultry trade, neglecting the much-less-regulated but not negligible illicit trade, and in its spatial resolution at the level of countries only. It is, however, worth mentioning that this analysis, i.e., the only one to date that includes dimensions of both domestic and wild birds, concluded that both sets of bird populations, i.e., poultry and wild birds, have contributed to the spread of HP-H5N1.

Mapping bird migration

The dimension of HP-H5N1 transmission that is perhaps most amenable to detailed mapping is that of bird distributions and movements. Given several centuries of study by ornithologists, as well as intense popular interest, birds rank among the best known of all major taxa (del Hoyo et al. 1992–2007), with detailed distributional information available for most species. Several studies have taken advantage of such information to develop insights into how wild bird movements could serve to disperse HP-H5N1 broadly across regions (Gilbert et al. 2006, Kilpatrick et al. 2006, Peterson et al. 2007, Winker et al. 2007), although a genuinely detailed synthesis has yet to be developed.

Fig. 4. Summary of wintering and breeding distributions of species that breed across both hemispheres in the Holarctic, but winter at least in part in the Americas; one species (*Larus ridibundus*) ranges considerably farther south in Russia, extending to areas that have indeed seen HP-H5N1 outbreaks. Color ramp indicates numbers of species (white = 0, darkest shade = 5 species). From Peterson et al. (2007).

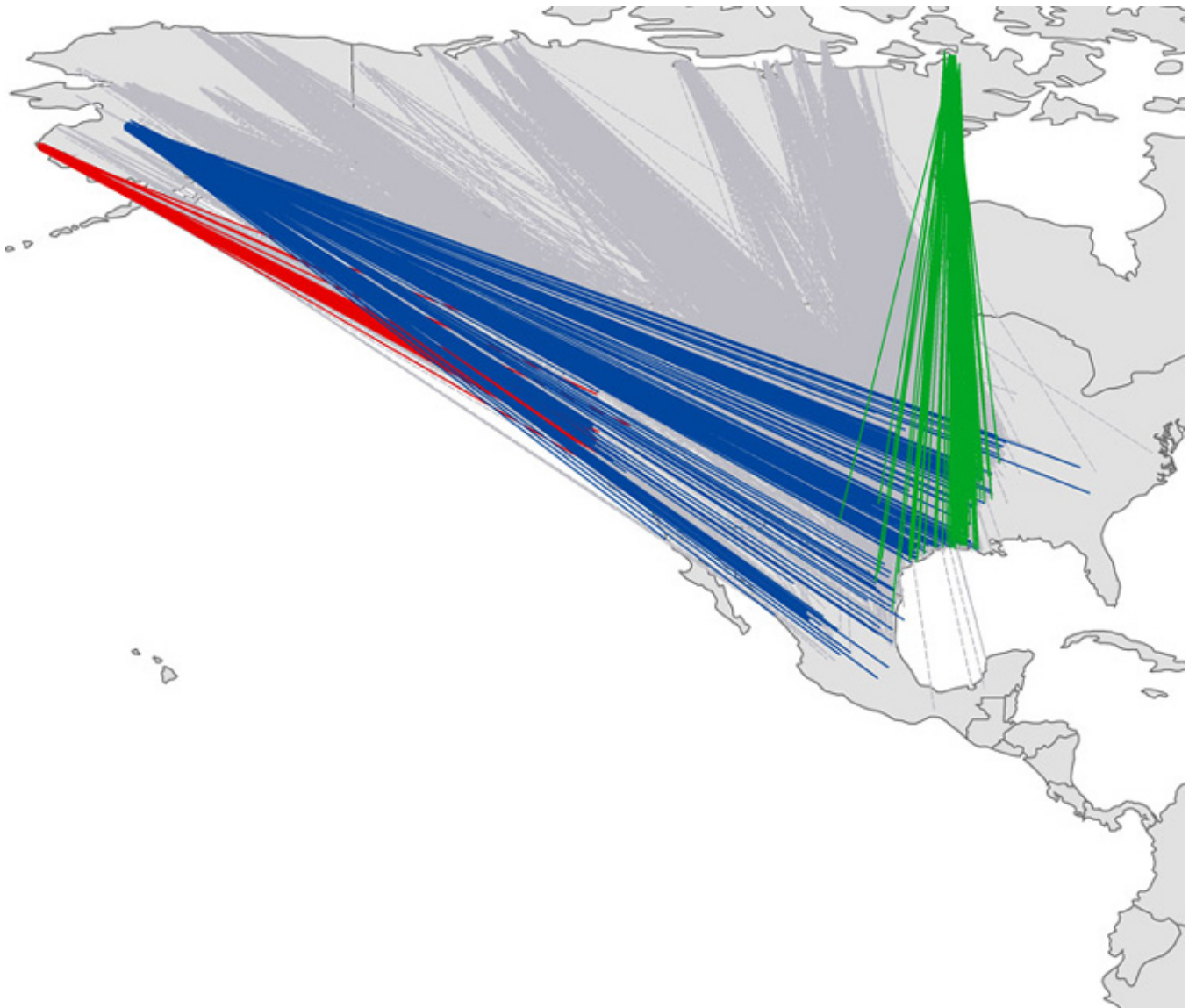


The global evaluation cited above (Kilpatrick et al. 2006) relied generally on information regarding bird movements along migratory pathways, which (as will be seen below) can be deceptively simple, and can miss important details. Similarly, the regional analysis of Gilbert et al. (2006) was also based on coarse-resolution flyway information on migratory bird movements. Reliance on such summary information can limit the spatial resolution of resulting information products. As such, in the following paragraphs, we review two recent, and more detailed, studies that deal with migration summaries on a species-by-species basis not constrained by the coarse detail and resolution of flyway information.

At coarse scales, an important suite of questions revolves around bird-mediated dispersal between continents. Although these questions have seen considerable speculation in recent commentaries (Rappole et al. 2000, Rappole and Hubalek 2006), real data and quantitative approaches can be more revealing. These questions were addressed recently in an HP-H5N1 context by Peterson et al. (2007). The question was how HP-H5N1, if it is being spread across Europe, Asia, and Africa by migratory

birds, could potentially reach the Americas. The conventional focus in the Americas has been on western Alaska as the most likely “port of entry” for the virus into the region (NBII 2006). Peterson et al. (2007), however, digitized summer and winter range maps for all of the 157 bird species that show regular seasonal movements between the two hemispheres, and illustrated that two very distinct patterns are present: birds that winter in southern Eurasia, breed across northern Eurasia, and have marginal breeding populations in northwestern or northeastern North America, i.e., the conventional focus, but also birds that winter in the Americas, but breed across northern North America and into northern Eurasia marginally (Fig. 4). The distributional patterns of these two sets of species contrast sharply, with the latter group ranging broadly southward into the Americas, suggesting that the western Alaska focus of attention may not be sufficient for effective HP-H5N1 monitoring. This study also illustrates vividly the perils of overreliance on summary data on migratory pathways, when individual species may behave in ways that do not ‘fit’ the general pattern comfortably.

Fig. 5. Illustration of the complexities of bird migration, when information on connectivity of areas is considered, even within a single species. Here, U.S. Bird Banding Laboratory data on banding and recovery events in breeding and winter seasons of Greater White-fronted Geese (*Anser albifrons*) are plotted on a map of North America. Records, i.e., lines connecting breeding and wintering records corresponding to banding and recovery of a single individual, not intended to reflect migratory routes, from particular areas of the breeding range are highlighted in different colors. Note that a significant portion of the blue lines also stops along the Pacific coast of North America, coincident with the winter destination of the red lines, and that none of the red lines extends farther east than the west coast.



At finer scales, the challenges of data resources become more acute. Ideally, patterns of connectivity of areas via bird migration would be mapped at fine scales, rather than just at the level of countries or flyways, but the technology for establishing such connectivity is only now being explored. Possibilities include stable isotope mapping (Farmer et al. 2004, Atkinson et al. 2005), fine-scale phylogeographic studies (Kelly et al. 2005), tracking of satellite transmitters attached to individual birds (Webster et al. 2002), and direct detections of connectivity from banding data (Belthoff and Gauthreaux 1991). Nonetheless, major challenges confront any broadscale efforts in this dimension.

To illustrate both the complexity of such applications and the need for probabilistic approaches to migratory connectivity, we show example patterns from Greater White-fronted Geese (*Anser albifrons*) in North America (Fig. 5) based on banding recoveries. Certainly, such analyses are subject to myriad caveats and qualifications, but the information provided for connectivity between breeding and wintering distributional areas for those species for which sample sizes are sufficient is almost unique. The resulting patterns are more complex than the simple flyway maps would suggest. In particular, while extreme coastal Alaska is connected via migration principally to the west coast of North America, individuals from areas just a few hundred kilometers inland, but still in western Alaska, range much more broadly across western North America. Only by combining information across many such individual species will a genuine and complete picture of migratory connectivity be possible.

CONCLUSIONS AND NEXT STEPS

The challenge of mapping risk of HP-H5N1 dispersal and transmission is clearly complex. Each element of the transmission cycle that can be mapped has significant caveats associated with it (see above): niche modeling of landscape suitability demands adequate identification of causal elements of landscape environments and how they actually affect HP-H5N1 transmission; poultry mapping requires more accurate summaries of official poultry distributions, but also resolution of the much more difficult challenges of mapping peasant-owned poultry and illicit poultry movements; and mapping of bird migration requires improved

protocols for integrating diverse data streams into a single overall picture. However, the only path to a genuine synthesis of the situation would include combination of all of these elements into a single analysis, i.e., broadscale connectivity via migratory birds, local and broadscale connectivity via poultry and poultry products, and local landscape suitability from ecological niche models. Clearly, the complexity of data, analyses, and interpretation in such a system would be daunting.

Nonetheless, the examples cited in this overview should, we hope, offer some stimulus. That is, important components of HP-H5N1 dispersal and transmission are amenable to analysis and mapping, and good templates for such mapping efforts are available already. As such, workers in particular situations and particular regions can take techniques already prototyped, and adapt them to particular challenges and questions. In this way, important portions of the HP-H5N1 risk mapping challenge can indeed be taken on as feasible steps.

Responses to this article can be read online at:
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LITERATURE CITED

- Alexander, D. J.** 2000. A review of avian influenza in different bird species. *Veterinary Microbiology* 74:3-13.
- Alexander, D. J.** 2007. Summary of avian influenza activity in Europe, Asia, Africa, and Australasia, 2002-2006. *Avian Diseases* 51:161-166.
- American Bird Conservancy (ABC).** 2005. *Avian influenza spreads: role of wild birds debated*. ABC. Available online at: <http://www.abcbirds.org/newsandreports/releases/051026.html>.

- Atkinson, P., A. Baker, R. Bevan, N. Clark, K. Cole, P. Gonzalez, J. Newton, L. Niles, and R. Robinson. 2005. Unravelling the migration and moult strategies of a long-distance migrant using stable isotopes: Red Knot *Calidris canutus* movements in the Americas. *Ibis* 147:738-749.
- Belthoff, J. R., and S. A. Gauthreaux, Jr. 1991. Partial migration and differential winter distribution of House Finches in the eastern United States. *Condor* 93:374-382.
- BirdLife International. 2006. *BirdLife statement on avian influenza*. BirdLife International. Available online at: http://www.birdlife.org/action/science/species/avian_flu/.
- Boender, G. J., T. J. Hagenaars, A. Bouma, G. Nodelijk, A. R. Elbers, M. C. de Jong, and M. van Boven. 2007. Risk maps for the spread of highly pathogenic avian influenza in poultry. *PLoS Computational Biology* 3:704-712.
- Boon, A. C. M., M. R. Sandbulte, P. Seiler, R. J. Webby, T. Songserm, Y. Guan, and R. G. Webster. 2007. Role of terrestrial wild birds in ecology of influenza A virus (H5N1). *Emerging Infectious Diseases* 13:1720-1724.
- Brown, J. D., D. E. Stallknecht, J. R. Beck, D. L. Suarez, and D. E. Swayne. 2006. Susceptibility of North American ducks and gulls to H5N1 highly pathogenic avian influenza viruses. *Emerging Infectious Diseases* 12:1663-1670.
- Capua, I., and D. J. Alexander. 2002. Avian influenza and human health. *Acta Tropica* 83:1-6.
- Chen, H., G. Deng, Z. Li, G. Tian, Y. Li, P. Jiao, L. Zhang, Z. Liu, R. G. Webster, and K. Yu. 2004. The evolution of H5N1 influenza viruses in ducks in southern China. *Proceedings of the National Academy of Sciences USA* 101:10452-10457.
- Chen, H., G. J. D. Smith, S. Y. Zhang, K. Qin, J. Wang, K. S. Li, R. G. Webster, J. S. M. Peiris, and Y. Guan. 2005. H5N1 virus outbreak in migratory waterfowl. *Nature* 436:191-192.
- Cox, N. J., and K. Subbarao. 2000. Global epidemiology of influenza: past and present. *Annual Review of Medicine* 51:407-421.
- del Hoyo, J., A. Elliot, and J. Sargatal. 1992-2007. *Handbook of the birds of the world*. Lynx Editions, Madrid, Spain.
- Ducatez, M. F., C. M. Olinger, A. A. Owoade, S. De Landtsheer, W. Ammerlaan, H. G. Niesters, A. D. Osterhaus, R. A. Fouchier, and C. P. Muller. 2006. Avian flu: multiple introductions of H5N1 in Nigeria. *Nature* 442:37.
- Farmer, A., M. Abril, M. Fernandez, J. Torres, C. Kester, and C. Bern. 2004. Using stable isotopes to associate migratory shorebirds with their wintering locations in Argentina. *Ornitologia Neotropical* 15:377-384.
- Feare, C. J., and M. Yasue. 2006. Asymptomatic infection with highly pathogenic avian influenza H5N1 in wild birds: how sound is the evidence? *Virology Journal* 3:96.
- Flint, P. L. 2007. Applying the scientific method when assessing the influence of migratory birds on the dispersal of H5N1. *Virology Journal* 4:132-134.
- Gaidet, N., T. Dodman, A. Caron, G. Balança, S. Desvaux, F. Goutard, G. Cattoli, F. Lamarque, W. Hagemeijer, and F. Monicat. 2007. Avian influenza viruses in water birds, Africa. *Emerging Infectious Diseases* 13:626-629.
- Gauthier-Clerc, M., C. Lebarbenchon, and F. Thomas. 2007. Recent expansion of highly pathogenic avian influenza H5N1: a critical review. *Ibis* 149:202-214.
- Gilbert, M., X. Xiao, P. Chaitaweesub, W. Kalpravidh, S. Premasathira, S. Boles, and J. Slingenbergh. 2007. Avian influenza, domestic ducks and rice agriculture in Thailand. *Agriculture, Ecosystems and Environment* 119:409-415.
- Gilbert, M., X. M. Xiao, J. Domenech, J. Lubroth, V. Martin, and J. Slingenbergh. 2006. Anatidae migration in the western palearctic and spread of highly pathogenic avian influenza H5N1 virus. *Emerging Infectious Diseases* 12:1650-1656.
- Goutard, F., F. Roger, J. Guitian, G. Balança, K. Argaw, A. Demissie, V. Soti, V. Martin, and D. Pfeiffer. 2007. Conceptual framework for AI risk assessment in Africa: the case of Ethiopia. *Avian Diseases* 51:504-506.

Guo, J., Y. Xue, S. Zhong, C. Cao, W. Cao, X. Li, and L. Fang. 2006. Preliminary study of avian influenza A infection using remote sensing and GIS techniques. Pages 9-12 in V. N. Alexandrov, G. D. van Albada, P. M. A. Sloot, and J. J. Dongarra, editors. *ICCS 2006 Proceedings* Springer, Berlin, Germany.

Hulse-Post, D. J., K. M. Sturm-Ramirez, J. Humberd, P. Seiler, E. A. Govorkova, S. Krauss, C. Scholtissek, P. Puthavathana, C. Buranathai, T. D. Nguyen, H. T. Long, T. S. Naipospos, H. Chen, T. M. Ellis, Y. Guan, J. S. Peiris, and R. G. Webster. 2005. Role of domestic ducks in the propagation and biological evolution of highly pathogenic H5N1 influenza viruses in Asia. *Proceedings of the National Academy of Sciences USA* 102:10682-10687.

Katz, J. M., X. Lu, A. M. Frace, T. Morken, S. R. Zaki, and T. M. Tumpey. 2000. Pathogenesis of and immunity to avian influenza A H5 viruses. *Biomedical Pharmacotherapy* 54:178-187.

Kelly, J. F., K. C. Ruegg, and T. B. Smith. 2005. Combining isotopic and genetic markers to identify breeding origins of migrant birds. *Ecological Applications* 15:1487-1494.

Kilpatrick, A. M., A. A. Chmura, D. W. Gibbons, R. C. Fleischer, P. P. Marra, and P. Daszak. 2006. Predicting the global spread of H5N1 avian influenza. *Proceedings of the National Academy of Sciences USA* 103:19368-19373.

Kou, Z., F. M. Lei, J. Yu, Z. J. Fan, Z. H. Yin, C. X. Jia, K. J. Xiong, Y. H. Sun, X. W. Zhang, X. M. Wu, X. B. Gao, and T. X. Li. 2005. New genotype of avian influenza H5N1 viruses isolated from tree sparrows in China. *Journal of Virology* 79:15460-15466.

Kwon, Y. K., S. J. Joh, M. C. Kim, Y. J. Lee, J. G. Choi, E. K. Lee, S. H. Wee, H. W. Sung, J. H. Kwon, M. I. Kang, and J. H. Kim. 2005. Highly pathogenic avian influenza in magpies (*Pica pica sericea*) in South Korea. *Journal of Wildlife Diseases* 41:618-623.

Mulatti, P., U. Kitron, A. Mannelli, N. Ferre, and S. Marangona. 2007. Spatial analysis of the 1999-2000 highly pathogenic avian influenza

(H7N1) epidemic in northern Italy. *Avian Diseases* 51:421-424.

Munster, V. J., C. Baas, P. Lexmond, J. Waldenstrom, A. Wallensten, T. Fransson, G. F. Rimmelzwaan, W. E. P. Beyer, M. Schutten, B. Olsen, A. D. M. E. Osterhaus, and R. A. M. Fouchier. 2007. Spatial, temporal, and species variation in prevalence of influenza A viruses in wild migratory birds. *PLoS Pathogens* 3:630-638.

National Biological Information Infrastructure (NBII). 2006. *National Avian Influenza Surveillance Information*. U.S. Geological Survey, Washington, D.C., USA. Available online at: <http://wildlifedisease.nbii.gov>.

Olsen, B., V. J. Munster, A. Wallensten, J. Waldenström, A. D. M. E. Osterhouse, and R. A. M. Fouchier. 2006. Global patterns of influenza A virus in wild birds. *Science* 312:384-388.

Parry, J. 2006. Children in Turkey die after contracting avian flu. *British Medical Journal* 332:67.

Peterson, A. T. 2006. Ecological niche modeling and spatial patterns of disease transmission. *Emerging Infectious Diseases* 12:1822-1826.

Peterson, A. T. 2008. Biogeography of diseases: a framework for analysis. *Naturwissenschaften* 95:483-491.

Peterson, A. T., B. W. Benz, and M. Papes. 2007. Highly pathogenic H5N1 avian influenza: entry pathways into North America via bird migration. *PLoS ONE* 2:e261. Available online at: <http://www.plosone.org/article/info:doi%2F10.1371%2Fjournal.pone.0000261>.

Pfeiffer, D. U., P. Q. Minh, V. Martin, M. Epprecht, and M. J. Otte. 2007. An analysis of the spatial and temporal patterns of highly pathogenic avian influenza occurrence in Vietnam using national surveillance data. *Veterinary Journal* 174:302-309.

Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* 3:349.

Rappole, J., S. R. Derrickson, and Z. Hubálek. 2000. Migratory birds and spread of West Nile virus

in the Western Hemisphere. *Emerging Infectious Diseases* 6:319-328.

Rappole, J. H., and Z. Hubalek. 2006. Birds and influenza H5N1 virus movement to and within North America. *Emerging Infectious Diseases* 12:1486-1492.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115-1123.

Soberón, J., and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2:1-10.

Sturm-Ramirez, K. M., T. Ellis, B. Bousfield, L. Bissett, K. Dyrting, J. E. Rehg, L. Poon, Y. Guan, M. Peiris, and R. G. Webster. 2004. Reemerging H5N1 influenza viruses in Hong Kong in 2002 are highly pathogenic to ducks. *Journal of Virology* 78:4892-4901.

Thanawongnuwech, R., A. Amonsin, R. Tantilertcharoen, S. Damrongwatanapokin, A. Theamboonlers, S. Payungporn, K. Nanthapornphiphat, S. Ratanamungklanon, E. Tunak, T. Songserm, V. Vivatthanavanich, T. Lekdumrongsak, S. Kesdangsakonwut, S. Tunhikorn, and Y. Poovorawan. 2005. Probable tiger-to-tiger transmission of avian influenza H5N1. *Emerging Infectious Diseases* 11:699-701.

Van Borm, S., I. Thomas, G. Hanquet, B. Lambrecht, M. Boschmans, G. Dupont, M. Decaestecker, R. Snacken, and T. van den Berg. 2005. Highly pathogenic H5N1 influenza virus in smuggled Thai eagles, Belgium. *Emerging Infectious Diseases* 11:702-705.

Webby, R. J., and R. G. Webster. 2001. Emergence of influenza A viruses. *Philosophical Transactions of the Royal Society of London B* 356:1817-1828.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76-83.

Webster, R. G., W. J. Bean, O. T. Gorman, T. M. Chambers, and Y. Kawaoka. 1992. Evolution and ecology of influenza A viruses. *Microbiology Review* 56:152-179.

Williams, R. A. J., F. O. Fasina, and A. T. Peterson. 2008. Predictable ecology and geography of avian influenza (H5N1) transmission in Nigeria and West Africa. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 102:471-479.

Winker, K., K. G. McCracken, D. D. Gibson, C. L. Pruett, R. Meier, F. Huettmann, M. Wege, I. V. Kulikova, Y. N. Zhuravlev, M. L. Perdue, E. Spackman, D. L. Suarez, and D. E. Swayne. 2007. Movements of birds and avian influenza from Asia into Alaska. *Emerging Infectious Diseases* 13:547-552.

World Organization for Animal Health (OIE). 2005. *Rapport de mission: mission to Russia to assess the avian influenza situation in wildlife and the national measures being taken to minimize the risk of international spread.* OIE. Available online at: <http://www.oie.int/downld/Missions/2005/ReportRussia2005Final2.pdf>.